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Antitranspirant-Induced Increases in Leaf Water Potential Increase Tuber Calcium and Decrease Tuber Necrosis in Water-Stressed Potato Plants[1]

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ABSTRACT

Experiments were undertaken with field-grown potato (*Solanum tuberosum* L.) plants to test the hypothesis that altering leaf:tuber water potential gradients within a plant subjected to low soil moisture will allow greater Ca accumulation in tubers and reverse Ca deficiency-related tuber necrosis. Antitranspirant formulations containing a wax emulsion and a spreader/sticker surfactant increased leaf water potential during a drought episode, significantly reducing the potential gradient that develops between leaf and tuber during a period of stress. Increased leaf water potential in treated plants was associated with decreased leaf Ca and increased tuber Ca. Tuber necrosis was found to be reduced in treated plants, thus increasing tuber quality.

Twenty-five years ago, Wiersum (11) presented evidence that, in a number of vegetable crops, a range of physiological disorders (such as bitter pit in apple, blackheart of celery, blossom-end rot in tomato, tip burn in cabbage and lettuce, and internal necrosis in potato) which are associated with localized Ca deficiencies in affected plant parts are caused by unfavorable internal Ψw[3] gradients. Ca is known to move in the plant exclusively in the xylem; this movement follows mass flow of transpirational water to the point of lowest Ψw (1). Wiersum (11) demonstrated that nonsenescing leaves with high transpiration rates (and concomitant low water potentials) act as strong sinks for Ca movement and restrict Ca supply to slowly transpiring organs such as fruits and tubers. It has been shown that water stress conditions exacerbate the disorder in potato, among other crops (5, 7, 8).

Although this class of Ca deficiency-related physiological disorders is recognized as an important limitation to optimum yield and quality in many horticultural crops (8), the amelioration of the disorder in plants exposed to even transitory water deficits in the field has proved problematic. In several field studies of potato, increased Ca fertilization has been noted to not necessarily result in an increase in tuber Ca (9) or a reduction in tuber necrosis (3). In pot-grown potato plants, Kratzke and Palta (4) showed that a 30-fold increase in the Ca concentration of a nutrient solution supplied to the basal roots of plants had no effect on tuber Ca.

The prevalence and severity of this disorder in potato plants exposed to water deficits serves as an excellent demonstration that a crop plant's water balance rarely reaches equilibrium. The low leaf Ψw which develops under stress should theoretically drive water movement from tubers (which have a higher Ψw) until no internal Ψw gradient exists between plant parts. Measurements of leaf and tuber water potentials in field-grown potato plants, however, have shown that the equilibrium state (*i.e.* tuber and leaves at the same Ψw) is never reached under typical field conditions, even during nighttime recovery from daytime transpiration-induced low leaf Ψw (2).

One objective of the study reported here was to demonstrate that altering internal water potential gradients by use of a foliar-applied antitranspirant on field-grown potato plants exposed to water deficits will, in fact, allow for greater Ca accumulation in tubers. A second objective was to determine whether Ca accumulation in the tuber could be increased sufficiently to significantly reduce the extent of tuber necrosis which occurs in a potato crop.

MATERIALS AND METHODS

Field Plot Design

Virus-free potato (*Solanum tuberosum* L.) seed pieces (cv "Atlantic") were obtained from the Maine Seed Foundation, treated with the fungicide Captan (46 g/kg tubers) and stored at 5°C until they were planted on April 28, 1988. Atlantic is the leading chipping cultivar grown in North America. Field plots were set up in a completely randomized design at the Rutgers University Vegetable Research Farm (New Brunswick, NJ) in a field that had Colt's Neck loam (sandy) soil with the following characteristics at 15 cm soil depth at the time of planting: pH, 4.7 ± 0.1 (mean ± SE); cation exchange capacity, 6.3 ± 0.1 meq/100 g soil; Ca, 1288 ± 90 kg/ha; and gravimetric water content, 0.152 g H_2O/g dry soil ($n = 5$ for all measurements). The soil Ca was relatively high as compared to similar studies (*e.g.* ref. 6). Cultural management (*e.g.* N-P-K fertilizer, pesticides) practices were used to maximize plant growth. Each plot was an area (6 × 3.6 m) containing four rows (0.9 m between rows) with tuber pieces planted 0.3 m apart within the rows at a soil depth of 15 cm; 80 plants were grown in each plot. All destructive measure-

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[3] Abbreviation: Ψw, water potential.

ments (Ψw and Ca analysis) were made on plants in one of the two center rows; all the plants in the other center row were harvested at the end of the growing season for yield measurements. There were four replicate plots for each treatment. The treatments applied to the plants in the field plot were three antitranspirant formulations and a control. The antitranspirant treatments were formulations of 2, 4, and 6% Folicote (an emulsion of wax polymers; Aquatrols Corp., Pennsauken, NJ) with 0.5% Biofilm (a spreader/sticker-type surfactant; Aquatrols Corp.). Antitranspirant formulations were applied at 1300 L/ha with a motorized backpack sprayer on the same day after planting (d 87) that a drought episode was imposed on all of the field plots by withholding irrigation. This drought episode lasted until d 105, when 0.4 cm of rain fell on the field plots. Plants in control plots were sprayed with water. Sufficient turbulence was caused by the air emitted from the sprayer in the leaf canopies to ensure thorough antitranspirant formulation coverage of abaxial and adaxial leaf surfaces.

Water Relations

Leaf and tuber Ψw were measured with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA) as described previously (2). All measurements were made at midday (11:00–13:30) on one plant per plot (four replications per treatment) periodically after treatment application and initiation of the drought episode (*i.e.* from d 87 onward). For tuber Ψw measurements, soil was carefully excavated from around a tuber without disturbing the stolen attachment. The tuber with several centimeters of stolen attached could be then excised and immediately placed in the pressure chambers. For leaf Ψw, leaflets from fully expanded, nonsenescing leaves in the top of the leaf canopy (*i.e.* exposed to full sunlight) were used for all measurements.

Ca and Internal Necrosis

Tubers and leaves (four per treatment) used for Ψw measurements on a given day were also used to measure leaf and tuber Ca during the growing season. Immediately after removal from the pressure chamber, the tissues were transferred to plastic bags and stored on ice until they could be weighed (for tubers, a 3- to 4-g section of medullary tissue from the center of the tuber bud apex end was sampled) and then left at 60°C to dry. Leaf and tuber section samples were then dry ashed and processed for Ca analysis according to the method of Kratzke and Palta (4) except that samples were ashed by heating to 500°C for 5 h (with an additional 4 h for oven [model F-A1738 Sybron/Thermolyne, Thermolyne Corp., Dubuque, IA] cooling) and $LaCl_3$ was not added to the HCl extracts. Samples were read on a model 2280 atomic absorption spectrophotometer (Perkin-Elmer, Norwalk, CT). In addition to the measurement of tissue Ca during the imposed drought episode, measurements were also taken at the end of the growing season (d 127 after planting). For these measurements, one leaf and five tubers were removed from the same plant (one plant per plot). Leaf and tuber Ca were calculated on a molar basis by ascertaining tissue water contents and assuming that all the measured Ca was in solution.

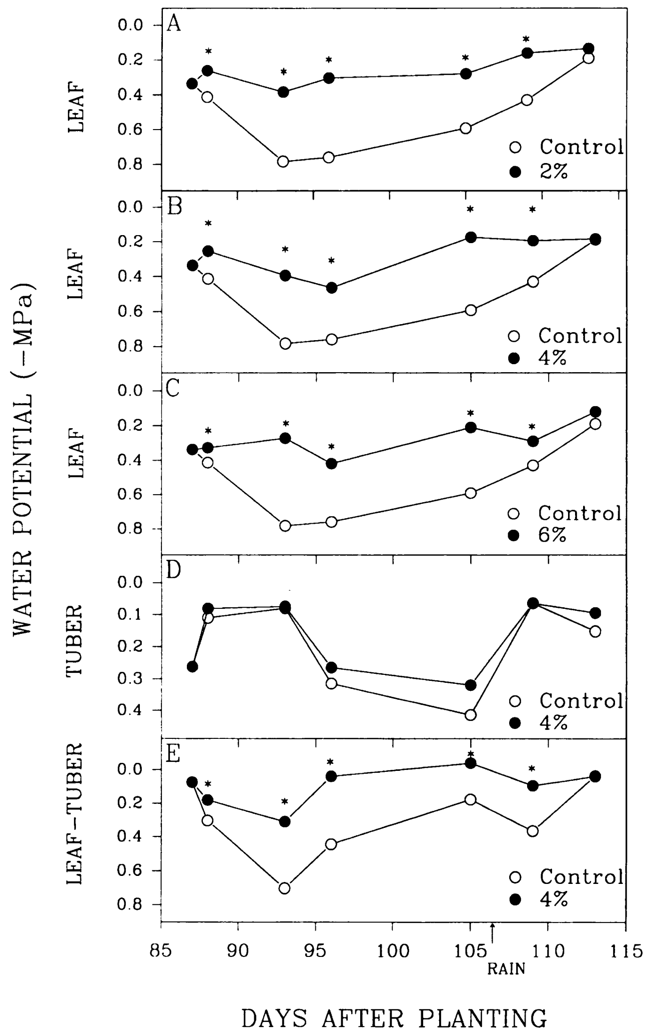

Figure 1. Antitranspirant effects on leaf and tuber Ψw in field-grown potato plants subjected to a drought episode. In all cases, data are presented as a comparison of control (○) values with values from an individual antitranspirant treatment (●). For a given day, an asterisk above these values indicates they are significantly different at the 5% level. Comparisons are presented between leaf Ψw measured in control plants and leaf Ψw of plants treated with antitranspirant formulations containing 2% (A), 4% (B), and 6% (C) Folicote. For tuber Ψw, a comparison is presented only between control plants and plants treated with 4% Folicote (D). For tuber Ψw, the data presented for the 4% Folicote treatment are representative of the values in plants treated with the other antitranspirant formulations; during the course of the experiment, tuber Ψw in all treatments was similar. The Ψw gradient between leaf and tuber is presented only for the control and 4% Folicote treatments (E). Again, the 4% Folicote treatment was representative of other antitranspirant treatments; leaf:tuber Ψw gradients were significantly affected by all the antitranspirant treatments (as compared with values in control plants) on all days that data were recorded except d 87 and d 113. On the evening of d 105 (after data were recorded) 0.4 cm of rain fell on the plots.

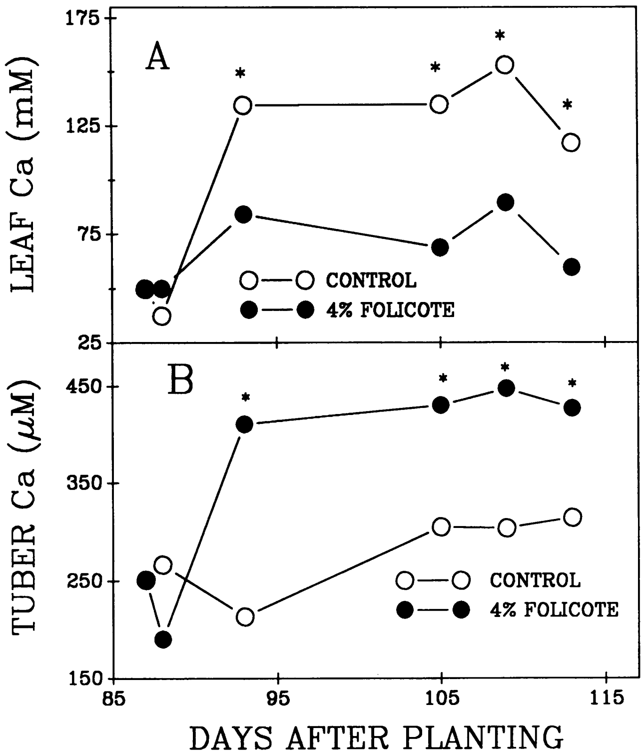

Figure 2. Antitranspirant effects on leaf (A) and tuber (B) calcium accumulation in field-grown potato plants during a drought episode. For a given day, an asterisk above the pair of data points indicates that they are significantly different at the 5% level. A comparison is presented only between control plants and plants treated with an antitranspirant formulation containing 4% Folicote; the data shown for 4% Folicote are representative of the effects of the other two antitranspirant formulations.

Internal necrosis of harvested tubers was evaluated visually, which is the standard procedure used to characterize this disorder in potatoes (*e.g.* ref. 10). The presence of the disorder in a particular tuber can be ascertained only by examining the internal flesh; necrosis is not evident on the epidermis of potato tubers. Harvested tubers were stored for 4 months at 4°C prior to necrosis evaluation. Previous reports indicate that tuber size is correlated with necrosis; the disorder is more extensive in large tubers (3). Therefore, necrosis was evaluated for several size categories of tubers: small (50–100 g fresh weight), medium (100–200 g), and large (>200 g). From the tubers harvested in each plot, 20 tubers of each size class were selected at random for necrosis evaluation. Each of these tubers was cut into eight equal pieces. Each tuber was scored for extent of necrosis, depending on what percentage of the eight pieces appeared to have brown, necrotic "flecks" in the internal tissue. Data presented as extent of necrosis, therefore, reflect the mean percentage of tissue in a tuber that appeared necrotic. The total number of tubers (of the 20 randomly selected tubers of each size class in each plot) that showed evidence of necrosis was also measured. This value, then, represented the percentage of tubers that showed any sign of necrosis. All data were evaluated for statistical significance using analysis of variance. Means separation at the 5% level was tested using the *t* test (for comparison of two treatments) or Duncan's multiple comparison test (when comparisons were made of more than two treatments).

RESULTS AND DISCUSSION

Prior to initiation of the field experiment, a number of control studies were undertaken with ionic, nonionic, and spreader/sticker surfactants in formulations with the wax emulsion Folicote. From these studies (data not shown), it was determined that aqueous formulations containing the surfactant Biofilm at 0.5% (v/v) and Folicote at either 2, 4, or 6% (v/v) were optimal in terms of restricting water loss from potato leaves without any apparent phytotoxic effects on plants. These three antitranspirant formulations (2, 4, and 6% Folicote, with 0.5% Biofilm) were selected for use in a study with field-grown potato plants.

Plants were grown under optimal cultural management conditions until d 87 after planting. Growth studies indicated that, by this day after planting, plants had reached maximum leaf area and were in the middle of the phase of rapid tuber growth (data not shown). Treatment application on d 87 coincided with the initiation of a drought episode in the field plots. As shown in Figure 1, A–C, leaf Ψw declined during this drought episode to a minimum of −0.8 MPa in control plots (*i.e.* in plants that were not treated with antitranspirant). This leaf Ψw decline in control plants was associated with high leaf resistance; there was, therefore, no significant difference in leaf resistance between control and antitranspirant-treated plants on any day that data were recorded. For example, on d 88, leaf resistance was 0.74 ± 0.07 s/cm in control plants. Plants treated with the antitranspirant formulations had a mean leaf resistance of 0.82 s/cm; this difference was not significant at $P \leq 0.05$. The fact that leaf resistance and, hence, transpiration were similar in treated and control plots as soon as 1 d into the drought episode, and throughout the entire measurement period (data not shown), suggests that the antitranspirant treatments likely had no substantial effect on the rate of soil water depletion.

Antitranspirant treatments were found to significantly increase leaf Ψw from the level found in control plants through-

Table I. *Leaf and Tuber Ca and Tuber Yields in Plants Harvested from Field Plots at the End of the Growing Season (127 d after Planting)*

For measurement of leaf and tuber Ca, one leaf and five tubers were sampled from one plant in each plot prior to destructive harvesting. No significant treatment effect on tuber yield was noted; treatment means for yields are therefore presented ± SE.

Treatment	Tuber Ca	Leaf Ca	Tuber Yields
	μM	*mM*	*mg/ha*
Control	242.3 a[a]	144.5 a[a]	45.6 ± 1.9
2% Folicote	396.3 ab	51.2 b	44.4 ± 2.9
4% Folicote	416.4 b	54.1 b	40.3 ± 3.3
6% Folicote	505.6 c	87.4 ab	41.9 ± 2.6

[a] Means within a column followed by the same letter are not significantly different at the 5% level.

Table II. *Relationship between Tuber Ca and Necrosis in Tubers of Varying Size*

All tubers used in this analysis were harvested from control field plots. Tubers of the three size categories were cut open and visually scored as necrotic or nonnecrotic (*i.e.* by the presence or absence of brown flecks or streaks in the internal medulla tissue). For each size category, samples were taken from the internal tissue of 10 necrotic or nonnecrotic tubers for Ca analysis. Tubers classified as large, medium, and small had weights of >200, 100 to 200, and 50 to 100 g, respectively.

Tuber Size	Ca Concentration	
	Nonnecrotic	Necrotic
	μM	
Large	292.6	237.2[a]
Medium	223.5	216.5
Small	227.7	130.5[a]

[a] The means in a row are significantly different at the 5% level.

out the drought episode. Leaf Ψw was maintained at or above −0.4 MPa, between d 87 and d 113 in plants treated with the antitranspirant formulations (Fig. 1, A-C). Tuber Ψw in both control and antitranspirant-treated plants remained at or above −0.4 MPa throughout the drought episode; there was no significant effect of the antitranspirant treatments on tuber Ψw (Fig. 1D). Comparison of tuber and leaf Ψw values indicated that, during the drought episode, large internal Ψw gradients between leaf and tuber developed in control plants (Fig. 1E). These drought-induced internal Ψw gradients were much reduced in antitranspirant-treated plants (Fig. 1E).

Studies were undertaken to determine whether treatment effects on internal Ψw gradients coincided with altered Ca distribution within treated plants. During the course of the drought episode, differences did develop in tuber and leaf Ca between control and treated plants (Fig. 2). The antitranspirant formulations were found to reduce leaf Ca (Fig. 2A) and increase tuber Ca (Fig. 2B) as compared with control plants. Significantly, the increased level of tuber Ca in treated plants as compared with the controls was still noted at the end of the growing season (Table I). Leaf Ca in treated plants was also found to be decreased from that found in control plants at the end of the growing season (Table I). It should be noted that the antitranspirant treatments had no significant effect on yield, although trends in the data suggested a minor (average of 7.5%) yield reduction in antitranspirant-treated plants (Table I). The data presented in Table I indicate that, when evaluated on a concentration (in the cell solution) basis, tuber Ca is much lower (*i.e.* by two orders of magnitude) than leaf Ca. These relatively low levels of tuber Ca are similar to the levels previously reported for Ca in the medullary tissue of potato tubers (4) and are typical of the Ca level found in such slowly transpiring plant organs (5, 11).

Studies were undertaken to determine whether altered Ca distribution in antitranspirant-treated plants was associated with a reduction in tuber necrosis. An analysis of medulla Ca in tubers visually scored as either necrotic or nonnecrotic established a correlation between internal necrosis and low tuber Ca (Table II). Necrotic tubers classified as large, medium, and small had lower tissue Ca than nonnecrotic tubers of the three sizes, although these differences were significant only in the large and small size categories. After a correlation between tuber Ca and necrosis had been established (Table II), effects of the antitranspirant treatments on tuber necrosis were evaluated. Increased tuber Ca in antitranspirant-treated plants was associated with a substantial reduction in tuber necrosis, when evaluated as either the average extent of tuber flesh that was affected (Fig. 3A) or the percentage of tubers showing signs of necrosis (Fig. 3B). When treatment means were averaged across all three size categories, the three antitranspirant formulations were found to reduce the extent of necrosis by 50% and to reduce the number of necrotic tubers by 40% as compared with tubers harvested from control plots. It should be noted that statistical analysis of the data presented in Figure 3 also demonstrated a significant association between tuber size and necrosis (analysis not shown). Larger tubers showed an increased extent of tuber necrosis. Previous investigators (5) noted that Ca deficiency-related disorders are most evident in rapidly expanding tissue, and Henninger *et al.* (3) speculated that tuber size is correlated with extent of necrosis in field-grown potato.

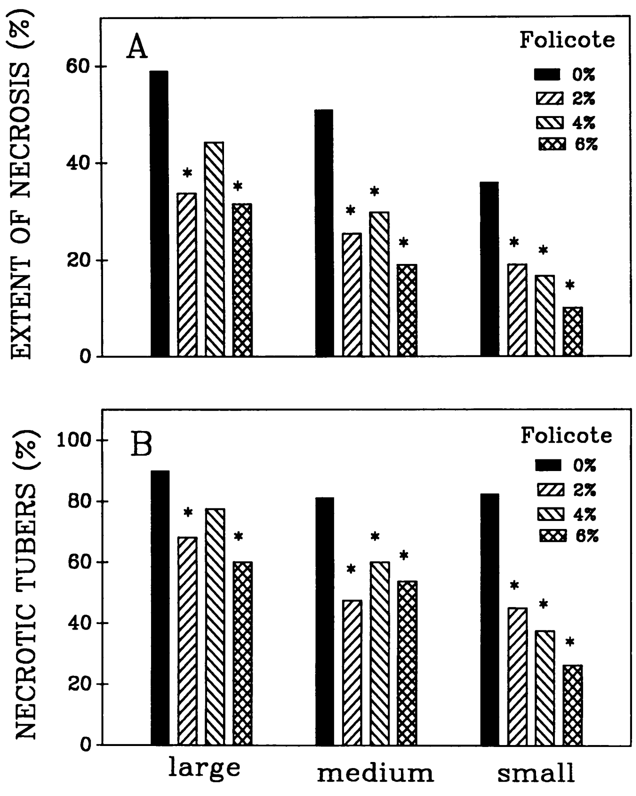

Figure 3. Effect of antitranspirant formulations on tuber necrosis in field-grown potato. Necrosis was evaluated by monitoring the average extent of necrosis evident in tubers (A) and by monitoring the proportion of the total tubers harvested from the field plots that showed any evidence of internal necrosis (B). In both cases, data are presented for treatment effects on tubers of the three size classifications. An asterisk over a vertical bar indicates that the mean of that treatment was significantly different from the control value for that size classification.

CONCLUSION

We conclude from the data presented in this report that wax emulsion-type leaf antitranspirants can substantially increase leaf Ψw in field-grown potato plants subjected to a period of low soil moisture. During such a stress period, low leaf Ψw creates Ψw gradients within a plant which likely restrict Ca accumulation in the developing tuber; antitranspirant application reverses (at least partially) this effect. Increases in tuber Ca in antitranspirant-treated plants (as compared with untreated controls) in this study were found to result in a reduction in tuber necrosis, thus enhancing crop quality without significantly reducing yield. These experiments support the hypothesis that altering leaf:tuber Ψw gradients can result in increased accumulation of Ca in developing tubers, thus reducing the extent of an important physiological disorder. These results also have practical significance, because the hypothesis was tested on field-grown plants cultured under commercial production conditions.

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